

IX.—On the Nauplius Stage of Prawns.

By C. SPENCE BATE, F.R.S.

It is now fifteen years since Fritz Müller published his memoir "Die Verwandlung der Garneelen," in the *Archiv f. Naturg.* 1863. In this he announced that he had discovered that the prawns, more especially mentioning *Penæus*, commenced life in a stage closely approximating to that in which the Cirripedes and some entomostracous Crustacea did, in that which is now known as the *Nauplius* form. Fritz Müller's high reputation as an accurate observer and philosophic naturalist induced carcinologists to accept his statement, although, as I stated when reporting on his memoir in the 'Zoological Record' for 1864, "in the chain there are one or two links wanting to make the connexion perfect," adding, in a note, that "since this passage has been in type, Dr. Müller informs us that the several links in the progressive development have been established by him, closer than, for want of space, he has been able to demonstrate in his work;" and I further added, at page 283 of the same 'Record,' "The difficulty of preserving the life of these delicate creatures has not yet been overcome. The newly hatched larva from the commonest and, we might assume, the hardiest crabs has not been preserved beyond the second stage. . . . It is therefore not to be demanded that Dr. Müller should succeed beyond the step at which others have stopped. It is only necessary for him to show assimilation of conditions to enable us to accept his conclusions."

Knowing that Captain Du Cane had, as far back as 1839, published, in the second volume of the 'Annals and Magazine of Natural History,' p. 168, pls. vi. & vii., the character and form of the young of *Palæmon*, and having also myself observed that the prawns on our coast, as far as I had examined them, exhibited no such character of metamorphosis, I, during my correspondence with Fritz Müller, suggested that the important link wanting was the connexion of the *Nauplius* with the parent, not, as he says, "the relation of the *Nauplius* with the *Zoëa*," and that until this was done the chain of evidence was not sufficient to compel acceptance, in the full sense that he proposed, of the opinion "that the *Nauplius* stage was the earliest form of the larval condition of prawns;" for, as he remarks in the paper translated in the 'Annals' for last month, his *Nauplius*, having been taken swimming freely in the sea, may not be the larva of *Penæus* at all.

In the important advance which the study of the Crustacea has of late taken, it is highly necessary that statements

that are to be accepted as facts should be established on observations that can leave us no doubt.

Unfortunately, on our coasts there is but one species of *Penæus* (*P. caramote*), and this appears to be rather a Mediterranean form that occasionally strays as far as our southern shores than a local species.

We might have supposed, as in the warmer seas several species are abundant, that some one would have been able during these last fifteen years to capture a specimen that was carrying ova so nearly approaching the period of hatching that Fritz Müller's conclusions might have been demonstrated: he would then not have had occasion to say, "if my *Nauplius* be not derived from a *Penæus*, and is not to become a *Penæus*, let my opponents tell me what possibly it can be."

Certainly exception should be taken to the word "opponent;" the only object that any truly sincere observer can have is to establish the truth. If the *Nauplius* form be that of a young of *Penæus* or any other prawn, it is only a question of time for us to know the fact. As yet the young of *Penæus* is not known; and Fritz Müller says that they who wish it demonstrated should tell him what his *Nauplius* is the young of. This can only be done when the larval forms of all prawns, including *Penæus*, are known by direct evidence. We shall therefore be approximating to the knowledge of this by showing what forms do not quit the ovum as larvæ in the *Nauplius* condition.

Some few years since, Dr. Power was attached to a regiment stationed in the Mauritius. During his period of residence in that island he occupied himself with collecting the various forms of Crustacea, and hatched many. These specimens he preserved, both adults and larvæ, and forwarded them to me. It formed the basis of a paper to the Royal Society, a short abstract of which appeared in the 'Proceedings' (No. 168, March 9th, 1876, p. 375*). Of the Macrurous forms we can say with confidence that neither the young of *Palæmon*, of which there is a freshwater species on the Island of Mauritius, as well as our European form, nor *Hippolyte*, *Caradina*, *Crangon*, *Alphæus*, *Homaralphæus*, n. g., *Homarus*, *Stenopus*, *Hymenocera*, *Palinurus*, *Squilla*, nor *Astacus* quits the ovum in the *Nauplius* condition. To these I can now add some of the deep-sea forms, including *Willemoësia*, that were taken during the 'Challenger' expedition. But this still leaves the ques-

* A year previous to the publication of Prof. Claus's memoir 'Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-Systems.'

tion unanswered, What can be the parent of Fritz Müller's *Nauplius*?

Why may it not be the larva of a Schizopod or of one of the parasitic Suctorina? The history of the development of neither of these has been worked out.

Metschnikoff states that *Euphausia* belongs to those Podophthalma that pass through a *Nauplius* condition. He says (Zeitschr. f. wissensch. Zoologie, vol. xix. p. 479), "that this Schizopod, in one stage of metamorphosis, has two pairs of swimming-feet, a peculiar carapace characteristic of *Euphausia*, and only the rudiments of the oral appendages and pleon. Although I knew but this single stage in the development of *Euphausia*, I was yet convinced that it by no means represented the earliest form of larva as it quits the ovum. I could, however, only hypothetically point to a six-legged transparent *Nauplius* as being the earlier larval condition of *Euphausia*."

This supposition he confirmed in a paper in the same journal in 1871, where he stated "that the year previously, being at Villafranca, he had the opportunity of examining a considerable number of freely-swimming *Euphausia*-larvæ;" and he further adds, "besides the larvæ which were in various stages, I fished up with Müller's net ova from which the larvæ were just ready to escape." The statement that he caught the *Nauplii* as free-swimming animals, and captured the ova with a net, raises a question in the mind yet as to the relation of the ova and freely-swimming *Nauplius* with their parent. But as I presume that *Euphausia* must have been present or Metschnikoff would not so positively have asserted their connexion, and as we are not aware of any Crustacea that deposit their ova until they have liberated the larvæ, we must suppose that in taking the one he captured the other. The ova of the Schizopoda being carried in a sac-like pouch and not attached to the pleopoda, as in the prawns, larvæ might be liberated in unequal degrees of development—although he says that, when the larvæ pass into an older stage, "all the larvæ of this last stage examined by me have lost with their moulting the indented margin to the carapace, which shows that I had to do with another species than *Euphausia Mülleri* (Claus)."

As far as the observations of all carcinologists enable us to decide, the form of larvæ, within generic relationship of their parents, is identical in all species. It may be fairly assumed that Claus's specimens, which were captured independently in the Atlantic, may be the young of some other nearly related Schizopod.

That *Euphausia* and its allies may pass through an immature stage like *Nauplius* is what might, though not generally

anticipated, have been thought probable since our knowledge of the development of *Mysis*.

The desirability of our knowing the form, structure, progressive growth, and parentage of these young forms is clearly demonstrated in Claus's recent beautiful work on the Genealogical Foundation of the Crustacean System, p. 54, in which he says, "In relation to the transformation of *Galathea*, which, on account of the half-bent tail, was placed with the Anomura, but, however, belongs decidedly to the long-tailed crawfish, unfortunately but little hitherto has become known to us. Couch has given an illustration, which has been reproduced by Bell, of a young recently hatched *Galathea*-larva, which confirmed the observation previously made by Rathke (Archiv f. Nat. 1848, p. 241), that it, as well as the larva of *Pagurus*, represents a higher degree of development than does the *Zoëa* of *Carcinus menas*, since, besides the two anterior double-branched pairs of legs, there is also a third jaw-foot present in the form of a still simple numerously jointed appendage—in contrast to the crab-*Zoëa*, which, as far as known in all groups and families of the Brachyura, want the posterior jaw-foot as an acting limb. There appears consequently the character of the prawn-*Zoëa* in the *Galathea*-larva, though in a weakened form, which, taken altogether, according to bodily structure, formation of antennæ, and jaws, might be placed among the long-tailed crawfish."

I do not know Rathke's figure of *Galathea* alluded to by Claus; but if it be not more clearly determined than the one referred to of Couch, it cannot be relied on for guidance as to the form of the animal, and is therefore valueless for general classification.

I have examined, and have in my possession, the young of both British and exotic *Galathea*, taken from the parent immediately after being hatched, which show that the larva of *Galathea* in its stage of development resembles *Porcellana* and *Pagurus* in having conditions which, as far as my own observation goes, are common to the Anomurous group. In development they are in advance of the *Zoëæ* of the Brachyura, but not so far as those of the Macrura. The *Zoëæ* of *Latreillia*, *Homola*, *Doripe*, and even *Dromia* have not been determined. I include *Dromia* among the undetermined forms; for the figure that Claus has given with a query as the young of *Dromia* approaches, according to my experience, nearer to the larva of *Gelasimus* than to any of the Anomurous group, while the larva of *Trichia*, a genus nearly allied to *Dromia*, assimilates to the Anomuran stage.

It appears scarcely desirable that any classification of a general character should be attempted upon larvæ that have been so imperfectly made known as that of *Galathea*. And, further, it appears to me that we have the forms of many types yet to determine before we dare hope to establish any permanent classification based on our knowledge of development.

Even so small a generalization as that which Claus has made, that the development of the cephalon and the pleon, with their respective appendages, anticipates that of the pereion with its limbs, is upset in the development of the common lobster, where the pereion and all the pereiopoda are well formed before a single appendage belonging to the pleon is seen. This is shown in the figure of the larva of *Homarus* which accompanied my paper read at the Royal Society in March 1876, as well as by the researches of Erdl, 1843, and the excellent memoir and illustrations of Mr. Sydney F. Smith on the American lobster (*Homarus americanus*, Edw.), 1872, Amer. Journ. Sci.

To return to the *Nauplius*, Fritz Müller says, "The child must surely have a father." True; but let it be the legitimate one. The young of *Pencæus* is not known. It appears to me rather remarkable that, among the numerous specimens of several species that have been brought home in the 'Challenger,' I have not been able to find one with ova attached.

There are conditions in some of the Peneids which show a variation in the structure of the reproductive apparatus from that of the more-known prawns that is suggestive of different habits; and I stoutly maintain that it is the duty of every embryologist, and of Fritz Müller in particular, to determine the larva of *Pencæus* before we can assert that the young of this genus or any of the prawn-groups can be said to be known to pass through a *Nauplius*-form.

Fritz Müller says that it cannot be the young of a Cirripede or rhizocephalous Crustacean. He bases this opinion on the formation of the heart, liver, and mandibles. All observation strongly supports the conclusion, arrived at long since by Milne-Edwards, that the structural detail of animals in their earliest stages corresponds more with their order than in their generic features. What do we know of the development of the Rhizocephala? What do we know of the development of *Sacculina*, *Cleistosoma*, *Peltogaster*, or any of the parasitic Suctorians? or as to what changes these undergo after the *Nauplius*-stage before they attach themselves as parasites to other Crustacea?

Dr. Power has shown us that in one of these (*Carcino-*

cystus *) the larva undergoes a metamorphosis as far as the cirripede pupa-stage before it is expelled from the ovisac of the parent; and this probably (either in the ovisac or after it has been liberated from it) is a stage in the progressive development of all the Suctorian tribe.

Metschnikoff says, in the paper already alluded to, "In conclusion, I must draw attention to a phenomenon which is common to the *Nauplius*-stage of *Euphausia* and *Penæus*; I mean the contemporaneous formation of several extremities succeeding the larval swimming-feet. It is remarkable that such a mode of formation is not observed in any Entomostraca which have been developed through a *Nauplius*-metamorphosis. I have examined in this relation the Cirripedes and Branchiopoda; and I became convinced that in these Crustacea the oral appendages are developed apart from the other extremities, as has been shown by Claus for the Copepodes."

If the oral appendages be not developed in direct sequence with the anterior appendages of the head, the evidence that the third pair of appendages in the *Nauplius* is the homologue of the adult mandible becomes vitiated.

Darwin has stated (p. 18, vol. i. 'Monograph of the Cirripedia') that the cirripede in the pupa stage has no mouth. "It may be called," he says, "a *locomotive pupa*; its whole organization is apparently adapted for the one great end of finding a proper site for its attachment and final metamorphosis." But Mr. Darwin, "underneath this slightly prominent and closed mouth, found all the masticatory organs of a cirripede in an immature condition." Later, when the animal arrives at its adult stage, it is furnished with oral appendages and uses them in eating.

If we compare the adult Cirripede with the adult Suctorian, the former, though attached to a foreign substance, has all the appendages of an animal in active existence. The latter is scarcely more than a sac, retaining its life apparently through its parasitic union with another. Its only capability appears to be the retention of a number of ova until they become matured. It has no appendage, oral or otherwise. The history of the development of this animal is unknown to us. Of what form is the male? and when does the female become impregnated? Is it before or after it has become attached to another animal? If after, the male must be a free-swimming animal; if before, then we must assume that there is some variation in its pupal condition from that of the normal cirri-

pede; and in this I am inclined to believe. Dr. Power in his drawing has figured the pupa of *Carcinocystus* so that it appears to have a long proboscidiiform mouth that is capable of being extended beyond the margin of the walls of the carapace, and so, we may presume, enabling it to feed; and it is difficult to imagine that an animal can grow to so large a size as this is in its adult condition if it had not the existence of an animal, both in feeding and selection, after it had passed beyond the *Nauplius*-condition.

Metschnikoff appears to me altogether to beg the question when he asserts that *Nauplius* is the larval form of *Penæus*, because it resembles that of *Euphausia* in certain conditions of development. After fully considering the subject, it appears to me that Fritz Müller's *Nauplius* may be the larval condition of a Schizopod, more or less related to *Euphausia*, or it may be the young of one of the Suctorian parasites, but that there is every reason to believe that it is not the young of any known prawn, and there is no evidence to determine its relation to *Penæus*.

X.—On Stromatopora.

By H. J. CARTER, F.R.S. &c.

IN my last paper ('Annals,' 1878, vol. i. p. 412) it is stated that the "hexactinellid structure," therein mentioned, "if not a sponge was still not a *Stromatopora*;" and further on, "at least" not of "the type to which I allude."

I am now able to solve the difficulty by having a short time since, through specimens of Babbicombe (Devonian) Limestone brought to this place (Budleigh-Salterton) for calcination, found that the "hexactinellid structure" is presented by *Stromatopora concentrica*, and just now, by the kind aid of Mr. Vicary, together with his books and specimens, have also been able to determine that the latter is *Caunopora*, Phill., 1841, = *Stromatopora placenta*, Lonsdale ap. Baily (see most satisfactory representations of both species in Phillips's 'Palæozoic Fossils of Cornwall, Devon, and West Somerset,' 1841, pl. x. figs. 21, 29).

These two points have been verified by an inspection of Mr. Vicary's great collection of *Stromatopora* to which I have before alluded, whereby it seems to me that, to expose the hexactinellid figure, the plane of section must be tangential to the curve of undulation in the layers of the *Stromatopora*, or horizontal to its summit—also that the more abrupt the un-